Title: Tree height and leaf drought tolerance traits shape growth responses across droughts in a temperate broadleaf forest

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Summary

- As climate change drives increased drought in many forested regions, mechanistic understanding of the factors conferring drought tolerance in trees is increasingly important. The dendrochronological record provides a window through which we can understand how tree size and traits shape growth responses to droughts.

- We analyzed tree-ring records for twelve species in a broadleaf deciduous forest in Virginia (USA) to test hypotheses on how tree height, microenvironment characteristics, and species' traits shaped drought responses across the three strongest regional droughts over a 60-year period.

- Drought tolerance (resistance, recovery, and resilience) decreased with tree height, which was strongly correlated with exposure to higher evaporative demand and solar radiation. The potentially greater rooting volume of larger trees did not confer a resistance advantage, but marginally increased recovery and resilience, in sites with low topographic wetness index. Drought tolerance was greater among species whose leaves experienced less shrinkage upon desiccation and lost turgor (wilted) at more negative water potentials.

- The tree-ring record reveals that tree height and leaf drought tolerance traits influenced growth responses during and after significant droughts in the meteorological record. As climate change-induced droughts intensify, tall trees with drought-sensitive leaves will be most vulnerable to immediate and longer-term growth reductions.

Key words: annual growth; crown exposure; drought; Forest Global Earth Observatory (ForestGEO); leaf drought tolerance traits; temperate broadleaf deciduous forest; tree height; tree-ring

Introduction

Forests play a critical global role in climate regulation (Bonan, 2008), yet there remains enormous uncertainty as to how the forest-dominated terrestrial carbon sink will respond to climate change (Friedlingstein et al., 2006). An important aspect of this uncertainty lies with physiological responses of trees to drought (Kennedy et al., 2019). In many forested regions around the world, the risk of severe drought is increasing (Trenberth et al., 2014; Dai et al., 2018), often despite increasing precipitation (Intergovernmental Panel on Climate Change, 2015; Cook et al., 2015). Droughts, intensified by climate change, have been affecting forests worldwide and are expected to continue as one of the most important drivers of forest change in the future (Allen et al., 2010, 2015; McDowell et al., 2020). Understanding forest responses to drought requires elucidation of how tree size, microenvironment, and species' traits jointly influence individual-level drought tolerance, defined here as a tree's ability to maintain growth during drought (resistance) and to recover to its pre-drought growth rate (resilience) (Lloret et al., 2011). Because the resistance and resilience of growth to drought are linked to trees' probability of surviving drought (DeSoto et al., 2020; Liu et al., 2019), understanding growth responses can also help elucidate which trees are most vulnerable to drought-induced mortality. However, it has proven difficult to resolve the many factors affecting tree growth during drought and the extent to which their influence is consistent across droughts. This is because available forest census data only rarely captures extreme drought, whereas tree-ring records capture multiple droughts but typically focus on only the largest individuals of one or a few species.

Many studies have shown that within and across species, large trees tend to be more affected by drought. Greater growth reductions (*i.e.*, lower drought resistance) in larger trees were first shown on a global scale by Bennett et al. (2015), and subsequent studies have reinforced this finding (*e.g.*, Gillerot et al., 2020). Although lower recovery and resilience of larger trees have also been observed (Hacket-Pain et al., 2016; Gillerot et al., 2020), in general we have much more limited understanding of how and why these scale with tree size.

physiological model of Trugman et al. (2018) predicts that recovery and resilience would not necessarily be lower, even in trees that will ultimately die.

Moreover, it has yet to be resolved which of several potential underlying mechanisms most strongly shape these trends in drought response. First, tree height itself may be a primary driver. Taller trees face the biophysical challenge of lifting water greater distances against the effects of gravity and friction (McDowell et al., 2011; McDowell and Allen, 2015; Ryan et al., 2006; Couvreur et al., 2018). Vertical gradients in stem and leaf traits–including smaller and thicker leaves (higher leaf mass per area, LMA), greater resistance to hydraulic dysfunction (*i.e.*, more negative water potential at 50% loss of hydraulic conductivity, more negative P50), and lower hydraulic conductivity at greater heights (Couvreur et al., 2018; Koike et al., 2001; McDowell et al., 2011)–enable trees to become tall (Couvreur et al., 2018). Greater stem capacitance (*i.e.*, water storage capacity) of larger trees may also confer resistance to transient droughts (Phillips et al., 2003; Scholz et al., 2011). Taller trees have wider conduits in the basal portions of taller trees, both within and across species (Olson et al., 2018; Liu et al., 2019) and throughout the conductive systems of angiosperms (Zach et al., 2010; Olson et al., 2014, 2018), which help maintain constant the resistance that would otherwise increase as trees grow taller. Wider xylem conduits plausibly make large trees more vulnerable to embolism during drought (Olson et al., 2018), and traits conducive to efficient water

transport may also lead to poor ability to recover from or re-route water around embolisms (Roskilly et al., 2019). **(here would be a good place to comment on resilience. "What may help the tree in competition, therefore, can also be a deteriment to drought resilience.")**

Larger trees may also have lower drought tolerance because of microenvironmental and ecological factors. Their crowns tend to occupy more exposed canopy positions, which are associated with higher evaporative demand (Kunert et al., 2017). Subcanopy trees tend to fare better specifically due to the benefits of a buffered environment (Pretzsch et al., 2018). Counteracting the liabilities associated with tall height, large trees tend to have larger root systems (Enquist and Niklas, 2002; Hui et al., 2014), potentially mitigating some of the biophysical challenges they face by allowing greater access to water. Larger root systems–if they grant access to deeper water sources–would be particularly advantageous in drier microenvironments (e.g., hilltops, as compared to valleys and streambeds) during drought. Finally, tree size-related responses to drought can be modified by species' traits and their distribution across size classes (Meakem et al., 2018; Liu et al., 2019). Understanding the mechanisms driving the greater relative growth reductions of larger trees during drought requires sorting out the interactive effects of height and associated exposure, root water access, and species' traits.

Debates have also arisen regarding the traits influencing tree growth responses to drought. Studies within temperate broadleaf forests have observed ring-porous species showing higher drought tolerance than diffuse-porous species (Friedrichs et al., 2009; Elliott et al., 2015; Kannenberg et al., 2019), but this distinction does not always hold (Martin-Benito and Pederson, 2015), nor does it hold in the global context (Wheeler et al., 2007; Olson et al., 2020), and it does not resolve differences among the many species within each category. Commonly-measured traits including wood density and leaf mass per area (LMA) have been linked to drought responses within some temperate deciduous forests (Abrams, 1990; Guerfel et al., 2009; Hoffmann et al., 2011; Martin-Benito and Pederson, 2015) and across forests worldwide (Greenwood et al., 2017). However, in other cases these traits could not explain drought tolerance (e.g., in a tropical rainforest; Maréchaux et al., 2019), or the direction of response was not always consistent. For instance, higher wood density has been associated with greater drought resistance at a global scale (Greenwood et al., 2017), but correlated negatively with tree performance during drought in a broadleaf deciduous forest in the southeastern United States (Hoffmann et al., 2011). Thus, the perceived influence of these traits on drought resistance may actually reflect indirect correlations with other traits that more directly drive drought responses (Hoffmann et al., 2011).

In contrast, hydraulic traits have direct physiological linkages to tree growth and mortality responses to drought. For instance, water potentials at which percent the loss of conductivity surpasses a certain threshold (e.g., P50 and P88, representing 50 and 88% loss of conductivity, respectively) and hydraulic safety margin (*i.e.*, difference between typical minimum water potentials and P50 or P88) correlate with drought performance across global forests (Anderegg et al., 2016). However, these are time-consuming to measure and therefore infeasible for predicting or modeling drought responses in highly diverse forests (*e.g.*, in the tropics). More easily-measurable leaf drought tolerance traits that have direct linkage to plant hydraulic function can explain variation in plant distribution and function (Medeiros et al., 2019). These include leaf area shrinkage upon desiccation (PLA_{dry}; Scoffoni et al., 2014) and the leaf water potential at turgor loss point (π_{tlp}), *i.e.,* the water potential at which leaf wilting occurs (Bartlett et al., 2016a; Zhu et al., 2018). Both traits correlate with hydraulic vulnerability and drought tolerance as part of unified plant hydraulic systems (Scoffoni et al., 2014; Bartlett et al., 2016a; Zhu et al., 2018; Farrell et al., 2017).

The abilities of both PLA_{dry} and π_{tlp} to explain the drought tolerance of tree growth remains untested.

Here, we examine how tree height, microenvironment characteristics, and species' traits collectively shape three metrics of drought tolerance: (1) resistance, defined as the ratio of annual stem growth in a drought year to that which would be expected in the absence of drought based on previous years' growth; (2) recovery, defined the ratio of post-drought growth to growth during the drought year; and (3) resilience, defined as the ratio of post-drought to pre-drought growth (Lloret et al., 2011). We test a series of hypotheses and associated specific predictions (Table 1) based on the combination of tree-ring records from the three strongest droughts over a 60-year period (1950 - 2009), species trait measurements, and census and microenvironmental data from a large forest dynamics plot in Virginia, USA. First, we focus on how tree size, alone and in its interaction with microenvironmental gradients, influences drought tolerance. We examine the contemporary relationship between tree height and microenvironment, including growing season meteorological conditions and crown exposure. We then test whether, consistent with most forests globally, larger-diameter, taller trees tend to have lower drought tolerance in this forest, which is in a region (eastern North America) represented by only two studies in the global review of (Bennett et al., 2015). We also test for an influence of potential access to available soil water, which should be greater for larger trees in dry but not in perpetually wet microsites. Finally, we focus on the role of species' traits, testing the hypothesis that species' traits--particularly leaf drought tolerance traits--predict drought tolerance. We test predictions that drought tolerance is higher in ring-porous than semi-ring and diffuse-porous species and that it is correlated with wood density–either positively (Greenwood et al., 2017) or negatively (Hoffmann et al., 2011) and positively correlated with LMA. We further test predictions that species with low PLA_{dry} and those whose leaves lose turgor at lower water potentials (more negative π_{tlp}) have higher tolerance.

Materials and Methods

Study site and microclimate

Research was conducted at the 25.6-ha ForestGEO (Forest Global Earth Observatory) study plot at the Smithsonian Conservation Biology Institute (SCBI) in Virginia, USA (38°53'36.6"N, 78°08'43.4"W; Fig. **S1**) (Bourg et al., 2013; Anderson-Teixeira et al., 2015a). SCBI is located in the central Appalachian Mountains near the northern boundary of Shenandoah National Park. Elevations range from 273 to 338 m above sea level with a topographic relief of 65m (Bourg et al., 2013). Climate is humid temperate, with mean annual temperature of 12.7°C and precipitation of 1005 mm yr^{-1} during our study period (1960-2009; source: CRU TS v.4.01; Harris et al., 2014). Dominant tree taxa within this secondary forest include *Liriodendron tulipifera*, oaks (*Quercus* spp.), and hickories (*Carya* spp.; Table 2).

Identifying drought years

We identified the three largest droughts within the time period 1950-2009, defining drought (Slette et al., 2019) as events with anomalously dry peak growing season climatic conditions. Specifically, we used the metric of Palmer Drought Severity Index (PDSI) during May-August (MJJA; Table S1), which were identified by Helcoski et al. (2019) as the months of the current year to which annual tree growth was most sensitive at this site. PDSI divisional data for Northern Virginia were obtained from NOAA (https://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp) in December 2017. Based on this, we identified the three strongest droughts during the study period (Figs. **1, S1**; Table S1).

165 The droughts differed in intensity and antecedent moisture conditions (Fig. **S1**, Table S1). The 1966
166 drought was preceded by two years of moderate drought during the growing season and severe to extreme
167 drought starting the previous fall. In August 1966, $PDSI$ reached its lowest monthly value (-4.82) of the
168 three droughts. The 1977 drought was the least intense throughout the growing season, and it was
169 preceded by 2.5 years of near-normal conditions, making it the mildest of the three droughts. The 1999
170 drought was preceded by wetter than average conditions until the previous June, but $PDSI$ plummeted
171 below -3.0 in October 1998 and remained below this threshold through August 1999. Following all three
172 droughts, $PDSI$ rebounded to near-normal conditions in September or October (Fig. **S1**).

173 *Data collection and preparation*

174 Within or just outside the ForestGEO plot, we collected data on a suite of variables including tree heights,
175 microenvironment characteristics, and species traits (Table 3). The SCBI ForestGEO plot was censused in
176 2008, 2013, and 2018 following standard ForestGEO protocols, whereby all free-standing woody stems $\geq$
177 1cm diameter at breast height (DBH) were mapped, tagged, measured at DBH, and identified to species
178 (Condit, 1998). From these census data, we used measurements of DBH from 2008 to calculate historical
179 DBH and data for all stems $\geq$ 10cm to analyze functional trait composition relative to tree height (all
180 analyses described below). Census data are available through the ForestGEO data portal
181 (www.forestgeo.si.edu).

182 We analyzed tree-ring data (xylem growth increment) from 571 trees representing the twelve dominant
183 species (Table 2; Fig. **S2**). Selected species were those with the greatest contributions to woody
184 aboveground net primary productivity ($ANPP_{stem}$) and together comprised 97% of study plot $ANPP_{stem}$
185 between 2008 and 2013 (Helcoski et al., 2019). Cores (one per tree) were collected within the ForestGEO
186 plot at breast height (1.3m) in 2010-2011 or 2016-2017. In 2010-2011, cores were collected from randomly
187 selected live trees of each species that had at least 30 individuals $\geq$ 10 cm DBH (Bourg et al., 2013).
188 Annual tree mortality censuses were initiated in 2014 (Gonzalez-Akre et al., 2016), and in 2016-2017, cores
189 were collected from all trees found to have died since the previous year's census. We note that drought was
190 probably not a cause of mortality for these trees, as monthly May-Aug $PDSI$ did not drop below -1.75 in
191 these years or the three years prior (2013-2017), and that trees cored dead displayed similar climate
192 sensitivity to trees cored live (Helcoski et al., 2019). Lagged drought-induced mortality would be unlikely,
193 given that the trees analyzed here lived at least 17-18 years past the most recent major drought (1999),
194 whereas the meta-analysis of Trugman et al. (2018) indicates that >10-year lags in drought-attributed
195 mortality are rare. Cores were sanded, measured, and crossdated using standard procedures, as detailed in
196 (Helcoski et al., 2019). The resulting chronologies (Fig. **1a**) were published in Zenodo (Gonzalez-Akre
197 et al., 2019).

198 For each cored tree, we combined tree-ring records and allometric equations of bark thickness to
199 reconstruct DBH for the years 1950-2009. Prior DBH was estimated using the following equation:

$$DBH_Y = DBH_{2008} - 2 * \left[r_{bark,2008} - r_{bark,Y} + \sum_{year=Y}^{2008} r_{ring,Y} \right]$$

200 Here, Y denotes the year of interest, r_{ring} denotes ring width derived from cores, and r_{bark} denotes bark
201 thickness, which was estimated from species-specific allometries based on the bark thickness data from the
202 site (Table S2; Anderson-Teixeira et al., 2015b).

6

Tree heights (H) were measured by several researchers for a variety of purposes between 2012 and 2019 (n=1,518 trees). Methods included direct measurements using a collapsible measurement rod on small trees (NEON, 2018) or a tape measure on recently fallen trees (this study); geometric calculations using clinometer and tape measure (Stovall et al., 2018a) or digital rangefinders (Anderson-Teixeira et al., 2015b; NEON, 2018); and ground-based LiDAR (Stovall et al., 2018b). Rangefinders used either the tangent method (Impulse 200LR, TruPulse 360R) or the sine method (Nikon ForestryPro) for calculating heights. Both methods are associated with some error (Larjavaara and Muller-Landau, 2013), but in this instance there was no clear advantage of one or the other. Measurements from the National Ecological Observatory Network (NEON) were collected near the ForestGEO plot following standard NEON protocol, whereby vegetation of short stature was measured with a collapsible measurement rod, and taller trees with a rangefinder (NEON, 2018). Species-specific height allometries were developed using log-log regression ($ln[H] \sim ln[DBH]$; Table S3). For species with insufficient height data to create reliable species-specific allometries (n=2, JUNI and FRAM), heights were calculated from an equation developed by combining the height measurements across all species. We then used these allometries to estimate H for each drought year, Y, based on reconstructed DBH_Y (Fig. **S3**).

To characterize how environmental conditions vary with height, data were obtained from the NEON tower located <1km from the study area via the neonUtilities package (Lunch et al., 2020). We used wind speed, relative humidity, and air temperature data, all measured over a vertical profile spanning heights from 7.2 m to above the top of the tree canopy (31.0 or 51.8m, depending on censor), for the years 2016-2018 (NEON, 2018). After filtering for missing and outlier values, we determined the daily minima and maxima, which we then aggregated at the monthly scale.

Crown position–a categorical variable classifying trees based on exposure to sunlight–was recorded for all cored trees that remained standing during the growing season of 2018 following the protocol of Jennings et al. (1999). Trees were classified as follows: *dominant* trees were defined as those with crowns above the general level of the canopy, *co-dominant* trees as those with crowns within the the canopy; *intermediate* trees as those with crowns below the canopy level, but illuminated from above; and *suppressed* as those below the canopy and receiving minimal direct illumination from above.

Topographic wetness index (TWI), used here as a metric of long-term mean moisture availability, was calculated using the dynatopmodel package in R (Fig. **S2**) (Metcalfe et al., 2018). Originally developed by Beven and Kirkby (1979), TWI was part of a hydrological run-off model and has since been used for a number of purposes in hydrology and ecology (Sørensen et al., 2006). TWI calculation depends on an input of a digital elevation model (DEM; ~3.7 m resolution from the elevatr package (Hollister, 2018)), and from this yields a quantitative assessment defined by how "wet" an area is, based on areas where run-off is more likely. From our observations in the plot, TWI performed better at categorizing wet areas than the Euclidean distance from the stream.

Species' trait data were collected in August 2018 (Tables 2-3; Fig. **S4**). We sampled small, sun-exposed branches up to eight meters above the ground from three individuals of each species in and around the ForestGEO plot. Sampled branches were re-cut under water at least two nodes above the original cut and re-hydrated overnight in covered buckets under opaque plastic bags before measurements were taken. Rehydrated leaves taken towards the apical end of the branch (n=3 per individual: small, medium, and large) were scanned, weighed, dried at 60° C for $\geq$ 48 hours, and then re-scanned and weighed. Leaf area was calculated from scanned images using the LeafArea R package (Katabuchi, 2019). *LMA* was

245 calculated as the ratio of leaf dry mass to fresh area. PLA_{dry} was calculated as the percent loss of area
246 between fresh and dry leaves. Wood density was calculated for ~1cm diameter stem samples (bark and pith
247 removed) as the ratio of dry weight to fresh volume, which was estimated using Archimedes' displacement.
248 We used the rapid determination method of Bartlett et al. (2012) to estimate osmotic potential at turgor
249 loss point (π_{tlp}). Briefly, two 4 mm diameter leaf discs were cut from each leaf, tightly wrapped in foil,
250 submerged in liquid nitrogen, perforated 10-15 times with a dissection needle, and then measured using a
251 vapor pressure osmometer (VAPRO 5520, Wescor, Logan, UT, USA). Osmotic potential (π_{osm}) given by
252 the osmometer was used to estimate (π_{tlp}) using the equation $\pi_{tlp} = 0.832\pi_{osm}^{-0.631}$ (Bartlett et al., 2012).

253 *Statistical Analysis*

254 For each drought year, we calculated metrics of drought resistance (Rt), recovery (Rc), and resilience (Rs),
255 following Lloret et al. (2011) (Table 3). We defined Rt as the ratio of basal area increment (BAI; *i.e.*,
256 change in cross-sectional area) during the drought year to the mean BAI over the five years preceding the
257 drought. Rc was defined as the ratio of mean BAI over the five years following the drought to BAI of the
258 drought year. Rs was defined as the ratio of mean BAI over the five years following the drought to that of
259 the five years preceding the drought. Thus, for all metrics, values <1 and >1 indicate growth reductions
260 and increases, respectively.

261 Because these metric could potentially be biased by directional pre-drought growth trends, we also tried an
262 intervention time series analysis (ARIMA, Hyndman et al., 2020) that predicted mean drought-year growth
263 based on trends over the preceding ten years and used this value in place of the five-year mean in
264 calculations of resistance (Rt_{ARIMA}= observed BAI/ predicted BAI). Rt and Rt_{ARIMA} were strongly
265 correlated (Fig. **S5**), and showed similar responses to the independent variables of interest (cf. Tables
266 S4-55, S8-S9). Visual review of the individual tree-ring sequences with the largest discrepancies between
267 these metrics revealed that Rt was less prone to unreasonable estimates than Rt_{ARIMA}. We therefore
268 determined that use of 5-year means, as described above, were more appropriate metrics than those based
269 on ARIMA projections.

270 Analyses focused on testing the predictions presented in Table 1 with Rt (or Rt_{ARIMA}), Rc, or Rs as the
271 response variable. Models were run for all drought years combined and for each drought year individually.
272 The general statistical model for hypothesis testing was a mixed effects model, implemented in the lme4
273 package in R (Bates et al., 2019). In the multi-year model, we included a random effect of tree nested
274 within species and a fixed effect of drought year to represent the combined effects of differences in drought
275 characteristics. Individual year models included a random effect of species. All models included fixed
276 effects of independent variables of interest (Tables 1,3) as specified below. All variables across all best
277 models had variance inflation factors between 1 and 1.045. We used Akaike information criterion with
278 correction for small sample sizes (AICc; see Brewer et al., 2016) to assess model selection, and
279 conditional/marginal R-squared to assess model fit as implemented in the AICcmodavg package in R
280 (Mazerolle and portions of code contributed by Dan Linden., 2019). Individual model terms were
281 considered significant when their addition to a model improved fit at ΔAICc $\geq$ 2.0, where ΔAICc is the
282 difference in AICc between models with and without the trait.

283 To avoid over-fitting models with five species traits (Table 3) across only 12 species, we did not include all
284 traits as fixed effects in a single linear mixed model, but rather conducted individual tests of each species
285 trait to determine the relative importance and appropriateness for inclusion in the main model. These tests
286 followed the model structure specified above, then added $ln[H]$ and $ln[TWI]$ to create a base model against

8

which we tested traits. Trait variables were considered appropriate for inclusion in the main model if their addition to the base model significantly improved fit for at least one metric of drought tolerance (*Rt*, *Rc*, or *Rs*; Tables S4,S6-S7). While we tested xylem porosity as a predictor (Table 1), we did not consider it appropriate for inclusion in the main model because of highly uneven distribution of species across categories (Table 2) and opposite drought responses of the only two diffuse-porous species (detailed below).

We then determined the top full models for predicting each dependent variable. To do so, we compared models with all possible combinations of candidate variables, including $ln[H]*ln[TWI]$ and species traits as specified above. We identified the full set of models within ΔAICc=2 of the best model (that with lowest AICc). When a variable appeared in all of these models and the sign of the coefficient was consistent across models, we viewed this as support for the acceptance/rejection of the associated prediction (Table 1). If the variable appeared in some but not all of these models, and its sign was consistent across models, we considered this partial support/rejection.

All analysis beyond basic data collection was performed using R version 3.6.2 (R Core Team, 2019). Other R-packages used in analyses are listed in the Supplementary Information (Appendix S1). All data, code, and results are available through the SCBI-ForestGEO organization on GitHub (https://github.com/SCBI-ForestGEO: SCBI-ForestGEO-Data and McGregor_climate-sensitivity-variation repositories), with static versions corresponding to data and analyses presented here archived in Zenodo (DOIs: 10.5281/zenodo.3604993 and *[TBD]*, respectively).

Results

Tree height and microenvironment

In the years for which we have vertical profiles in climate data (2016-2018), taller trees–or those in dominant crown positions– were generally exposed to higher evaporative demand during the peak growing season months (May-August; Fig. **2**). Specifically, maximum daily wind speeds were significantly higher above the top of the canopy (40-50m) than within and below (10-30m) (Fig. **2a**). Relative humidity was also somewhat lower during June-August, ranging from ~50-80% above the canopy and ~60-90% in the understory (Fig. **2b**). Air temperature did not vary consistently across the vertical profile (Fig. **2c**).

Crown position varied as expected with height (dominant > co-dominant > intermediate > suppressed), but with substantial variation (Fig. **2d**). There were significant differences in height across all crown position classes (Fig. **2d**). A comparison test between height and crown position data from the most recent ForestGEO census (2018) revealed a correlation of 0.73.

Community-level drought responses

At the community level, cored trees showed substantial growth reductions in all three droughts, with a mean *Rt* of 0.86 in 1966 and 1999, and 0.84 in 1977 (Fig. **1b**). Across the entire study period (1950-2009), the focal drought years were the three years with the largest fraction of trees exhibiting $Rt \leq 0.7$. Specifically, in each drought, roughly 30% of the cored trees had growth reductions of $\geq 30\%$ ($Rt \leq 0.7$): 29% in 1966, 32% in 1977, and 27% in 1999. However, some individuals exhibited increased growth, *i.e.*, $Rt > 1.0$: 26% of trees in 1966, 22% in 1977, and 26% in 1999. Recovery was generally strong and complete, with *Rc* averaging 1.55 in 1966, 1.42 in 1977, and 1.34 in 1999 (Fig. **S6**) and *Rs* averaging 1.28 in 1966, 1.19 in 1977, and 1.12 in 1999 (Fig. **1c**).

In the context of the multivariate model, Rt did not vary across drought years. That is, drought year as a variable did not appear in any of the top models – *i.e.*, models that were statistically indistinguishable (ΔAICc$<$2) from the best model (see footnotes on Tables S8-S9). In contrast, "drought year" varied for both Rc and Rs, and were present in all of the top models for the combined scenario (Tables S10-S11). Between both metrics, coefficients for "drought year" were highest in 1966, intermediate in 1977, and lowest in 1999.

Tree height, microenvironment, and drought tolerance

Taller trees (based on H in the drought year) showed stronger growth reductions during drought (i.e., lower Rt) and less resilience following drought (i.e., lower Rc and Rs; Table 1; Fig. **4**). Specifically, for Rt, $ln[H]$ appeared, with negative coefficient, in the best model (ΔAICc$=0$) and all top models when evaluating the three drought years together (Tables S8-S9). The same held true for 1966 individually, but there was no significant effect of $ln[H]$ for 1977 or 1999 individually. For Rc, $ln[H]$ appeared, with negative coefficient, in the best model without a $ln[H]*ln[TWI]$ interaction, for the three drought years together and for 1977, but not for 1966 or 1999. For Rs, again considering the best models without a $ln[H]*ln[TWI]$ interaction, there was a negative effect of $ln[H]$ for the three drought years together and for 1966 and 1977, and a non-significant negative trend in 1999.

Trees in drier microsites showed greater growth declines during drought; i.e., Rt had a significantly negative response to $ln[TWI]$ across all drought years combined, and in 1977 and 1999 individually (Fig. **4**, Table S8-S9). The $ln[H]*ln[TWI]$ interaction was never significant, and had a positive sign in any top Rt models in which it appeared (Tables 1, S8-S9), rejecting the hypothesis that smaller trees (presumably with smaller rooting volume) are more susceptible to drought in microenvironments with a deeper water table. In contrast, $ln[TWI]$ did not appear in any of the best models for Rc or Rs (combined of for individual years), except in interaction with $ln[H]$ (Fig. 4, Tables S10-S11). Negative $ln[H]*ln[TWI]$ interactions appeared in the best models for both Rc and Rs for all years combined, as well as in one individual year for each (1966 for Rc, 1977 for Rs). This implies that small trees had greater recovery and resilience in wetter microhabitats, whereas large trees had greater recovery and resilience in dry microhabitats.

Species' traits and drought tolerance

Species, as a factor in ANOVA, had significant influence (p$<$0.05) on all traits (wood density, LMA, PLA_{dry}, and π_{tlp}), with more significant pairwise differences for wood density and PLA_{dry} than for LMA and π_{tlp} (Table 2, Fig. **S4** as characterized by the agricolae package de Mendiburu (2020)). Drought tolerance also varied across species, overall and in each drought year (Figs. **3, S7**). Species with overall lowest and highest Rt and Rs were, respectively, *Liriodendron tulipifera* (mean $Rt = 0.66$, mean $Rs = 1.04$) and *Fagus grandifolia* (mean $Rt = 0.99$; mean $Rs = 1.65$). These two species–notably the only two diffuse-porous species in our study–differed significantly from one another in Rt and Rs in each drought year (Fig. **3**).

Wood density, LMA, and xylem porosity were all poor predictors of drought tolerance (Tables 1,S4-S5). Wood density and LMA were never significantly associated with Rt, Rc, or Rs in the single-variable tests and were therefore excluded from the full models. Xylem porosity had no significant influence on Rt or Rs in models for all droughts combined (Tables S4, S7). In contrast, Rc was significantly higher in diffuse- and semi-ring porous species than in ring-porous species (Table S6, Fig. 3).

Drought resistance and resilience, but not recovery, were negatively correlated with PLA_{dry} and π_{tlp} (Fig.

367 **4**; Tables 1, S4-S11). For Rt, PLA_{dry} had a significant influence, with negative coefficient, in top models
368 for the three droughts combined and for the 1966 drought individually (Fig. **4**; Tables S8-S9). It was also
369 included in some of the top models for 1999 (Tables S8-S9). π_{tlp} was included with a negative coefficient in
370 the best model for the combined droughts scenario and for the 1977 drought individually (Fig. **4**; Table
371 S8), although its influence was not significant at ΔAICc<2. It was also included in some of the top models
372 for 1999 (Tables S8-S9).

373 Recovery was not significantly correlated with either PLA_{dry} or π_{tlp}. There was only one best Rc model
374 containing one of these terms (π_{tlp} in 1977 drought), but in no instance was one of these terms included in
375 all top models (i.e., at ΔAICc<2).

376 For Rs, PLA_{dry} was in the best models for the three droughts combined and for the 1966 drought
377 individually, and some of the top models for 1977 and 1999 (Fig. **4**; Table S11); however, its effects were
378 not significant at ΔAICc<2. π_{tlp} was in the best models for the three droughts combined and for 1966 and
379 1999 individually, and in one of the top models for 1977 (Fig. **4**; Table S11). However, its effects were
380 significant at ΔAICc<2 for 1999 only.

Discussion

382 Tree height, microenvironment, and leaf drought tolerance traits shaped tree growth responses across three
383 droughts at our study site (Table 1, Fig. **4**). The greater susceptibility of larger trees to drought, similar to
384 forests worldwide (Bennett et al., 2015), was driven primarily by their height (Stovall et al., 2019). Taller
385 height was likely a liability in itself, and was also associated with greater exposure to conditions that would
386 promote water loss and heat damage during drought (Fig. **2**). There was no evidence that greater
387 availability of, or access to, soil water availability increased drought resistance; in contrast, trees in wetter
388 topographic positions had lower Rt (Zuleta et al., 2017; Stovall et al., 2019), and the larger potential
389 rooting volume of large trees provided no advantage in the drier microenvironments. The negative effect of
390 height on Rt held after accounting for species' traits, which is consistent with recent work finding height
391 had a stronger influence on mortality risk than forest type during drought (Stovall et al., 2020). Drought
392 tolerance was not consistently linked to species' LMA, wood density, or xylem type (ring- vs. diffuse
393 porous), but was negatively correlated with leaf drought tolerance traits (PLA_{dry}, π_{tlp}). This is the first
394 study to our knowledge linking PLA_{dry} and π_{tlp} to growth reduction during drought. The directions of
395 these responses were consistent across droughts (Table S8), supporting the premise that they were driven
396 by fundamental physiological mechanisms. However, the strengths of each predictor varied across droughts
397 (Fig. **4**; Tables S8-S9), indicating that drought characteristics interact with tree size, microenvironment,
398 and traits to shape which individuals are most affected. These findings advance our knowledge of the
399 factors that make trees vulnerable to stem growth declines during drought and, by extension, likely make
400 them more vulnerable to mortality (Sapes et al., 2019).

401 The droughts considered here were of a magnitude that has occurred with an average frequency of
402 approximately once every 10-15 years (Fig. **1a**, Helcoski et al., 2019) and had substantial but not
403 devastating impacts on tree growth (Figs. **1b**). These droughts were classified as severe ($PDSI < -3.0$;
404 1977) or extreme ($PDSI < -4.0$; 1966, 1999) at our site and have been linked to tree mortality in the
405 eastern United States (Druckenbrod et al., 2019). However, extreme, multiannual droughts such as the
406 so-called "megadroughts" of this type that have triggered massive tree die-off in other regions (e.g., Allen

11

et al., 2010; Stovall et al., 2019) have not occurred in the Eastern United States within the past several decades (Clark et al., 2016). Of the droughts considered here, the 1966 drought, which was preceded by two years of dry conditions (Fig. **S1**), severely stressed a larger portion of trees (Fig. **1b**). The tendency for large trees to have lowest resistance was most pronounced in this drought, consistent with other findings that this physiological response increases with drought severity (Bennett et al., 2015; Stovall et al., 2019). Across all three droughts, the majority of trees experienced reduced growth, but a substantial portion (e.g., short understory trees, species with drought resistant traits; Fig. **4**) had increased growth (Fig. **1b**), consistent with prior observations that smaller trees can exhibit increased growth rates during drought (Bennett et al., 2015). It is likely because of the moderate impact of these droughts, along with other factors influencing tree growth (e.g., stand dynamics), that our best models characterize only a modest amount of variation in *Rt*: 11-12% for all droughts combined, and 18-25% for each individual drought (Table S8).

Consistent with studies in other forests worldwide (Bennett et al., 2015), taller trees in this forest exhibited lower drought resistance–*and also recovery and resilience.* Mechanistically, this is consistent with, and reinforces, previous findings that it is impossible for trees to efficiently transport water to great heights and simultaneously maintain strong resistance and resilience to drought-induced embolism (Olson et al., 2018; Couvreur et al., 2018; Roskilly et al., 2019). Taller trees also face dramatically different microenvironments (Fig. **2**). They are exposed to higher wind speeds and lower humidity (Fig. **2a-b**), resulting in higher evaporative demand. Unlike other temperate forests where modestly cooler understory conditions have been documented (Zellweger et al., 2019), particularly under drier conditions (Davis et al., 2019), we observed no significant variation in air temperatures across the vertical profile (Fig. **2c**). More critically for tree physiology, leaf temperatures can become significantly elevated over air temperature under conditions of high solar radiation and low stomatal conductance (Campbell and Norman, 1998; Rey-Sánchez et al., 2016). Under drought, when air temperatures tend to be warmer, direct solar radiation tends to be higher (because of less cloud cover), and less water is available for evaporative cooling of the leaves, trees with sun-exposed crowns may not be able to simultaneously maintain leaf temperatures below damaging extremes and avoid drought-induced embolism. Indeed, previous studies have shown lower drought resistance in more exposed trees (Liu and Muller, 1993; Suarez et al., 2004; Scharnweber et al., 2019). Unfortunately, collinearity between height and crown exposure in this study (Fig. **2d**) makes it impossible to confidently partition causality. Additional research comparing drought responses of early successional and mature forest stands, along with short and tall isolated trees, would be valuable for more clearly disentangling the roles of tree height and crown exposure.

Belowground, taller trees would tend to have larger root systems (Enquist and Niklas, 2002; Hui et al., 2014), but this does not necessarily imply that they have greater access to or reliance on deep soil-water resources that may be critical during drought. While tree size can correlate with the depth of water extraction (Brum et al., 2019), the linkage is not consistent. Shorter trees can vary broadly in the depth of water uptake (Stahl et al., 2013), and larger trees may allocate more to abundant shallow roots that are beneficial for taking up water from rainstorms (Meinzer et al., 1999). Moreover, reliance on deep soil-water resources can actually prove a liability during severe and prolonged drought, as these can experience more intense water scarcity relative to non-drought conditions (Chitra-Tarak et al., 2018). In any case, the potentially greater access to water did not override the disadvantage conferred by height–and, in fact, greater moisture access in non-drought years (here, higher TWI) appears to make trees more sensitive to drought (Zuleta et al., 2017; Stovall et al., 2019). This may be because moister habitats would tend to

450 support species and individuals with more mesophytic traits (Bartlett et al., 2016b; Mencuccini, 2003;
451 Medeiros et al., 2019), potentially growing to greater heights [e.g., Detto et al. (2013), and these are then
452 more vulnerable when drought hits. The observed height-sensitivity of Rt, together with the lack of
453 conferred advantage to large stature in drier topographic positions, agrees with the concept that
454 physiological limitations to transpiration under drought shift from soil water availability to the
455 plant-atmosphere interface as forests age (Bretfeld et al., 2018), such that tall, dominant trees are the most
456 sensitive in mature forests. Again, additional research comparing drought responses across forests with
457 different tree heights and water availability would be valuable for disentangling the relative importance of
458 above- and belowground mechanisms across trees of different size.

459 The development of tree-ring chronologies for the twelve most dominant tree species at our site (Helcoski
460 et al., 2019; Bourg et al., 2013) gave us the sample size to compare historical drought responses across
461 species (Fig. **3**) and associated traits at a single site (see also Elliott et al., 2015). Our study reinforced
462 current understanding (see Introduction) that wood density and LMA are not reliably linked to drought
463 resistance (Table 1). Contrary to several previous studies in temperate deciduous forests (Friedrichs et al.,
464 2009; Elliott et al., 2015; Kannenberg et al., 2019), we did not find an association between xylem porosity
465 and drought resistance, as the two diffuse-porous species, *Liriodendron tulipifera* and *Fagus grandifolia*,
466 were at opposite ends of the Rt spectrum (Fig. **3**). While the low Rt of *L. tulipifera* is consistent with
467 other studies (Elliott et al., 2015), the high Rt of *F. grandifolia* contrasts with studies identifying diffuse
468 porous species in general (Elliott et al., 2015; Kannenberg et al., 2019), and the genus *Fagus* in particular
469 (Friedrichs et al., 2009), as drought sensitive. There are two potential explanations for this discrepancy.
470 First, other traits can and do override the influence of xylem porosity on drought resistance. Ring-porous
471 species are restricted mainly to temperate deciduous forests, while highly drought-tolerant diffuse-porous
472 species exist in other biomes (Wheeler et al., 2007). *Fagus grandifolia* had intermediate π_{tlp} and low
473 PLA_{dry} (Fig. **S4**), which would have contributed to its drought resistance (Fig. **4**; see discussion below).
474 A second explanation of why *F. grandifolia* trees at this particular site had higher Rt is that the sampled
475 individuals, reflective of the population within the plot, are generally shorter and in less-dominant canopy
476 positions compared to most other species (Fig. **S4**). The species, which is highly shade-tolerant, also has
477 deep crowns (Anderson-Teixeira et al., 2015b), implying that a lower proportion of leaves would be affected
478 by harsher microclimatic conditions at the top of the canopy under drought (Fig. **2**). Thus, the high Rt of
479 the sampled *F. grandifolia* population can be explained by a combination of fairly drought-resistant leaf
480 traits, shorter stature, and a buffered microenvironment.

481 Concerted measurement of tree-rings and leaf drought tolerance traits of emerging importance (Scoffoni
482 et al., 2014; Bartlett et al., 2016a; Medeiros et al., 2019) allowed novel insights into the role of drought
483 tolerance traits in shaping drought response. The finding that PLA_{dry} and π_{tlp} can be useful for predicting
484 drought responses of tree growth (Fig. **4**; Table 1) is both novel and consistent with previous studies
485 linking these traits to habitat and drought tolerance. Previous studies have demonstrated that π_{tlp} and
486 PLA_{dry} are physiologically meaningful traits linked to species distribution along moisture gradients
487 (Maréchaux et al., 2015; Fletcher et al., 2018; Medeiros et al., 2019; Simeone et al., 2019; Rosas et al., 2019;
488 Zhu et al., 2018), and our findings indicate that these traits also influence drought responses. Furthermore,
489 the observed linkage of π_{tlp} to Rt in this forest aligns with observations in the Amazon that π_{tlp} is higher
490 in drought-intolerant than drought-tolerant plant functional type. Further, it adds support to the idea that
491 this trait is useful for categorizing and representing species' drought responses in models (Powell et al.,
492 2017). Because both PLA_{dry} and π_{tlp} can be measured relatively easily (Bartlett et al., 2012; Scoffoni

et al., 2014), they hold promise for predicting drought growth responses across diverse forests. The importance of predicting drought responses from species traits increases with tree species diversity; whereas it is feasible to study drought responses for all dominant species in most boreal and temperate forests (e.g., this study), this becomes difficult to impossible for species that do not form annual rings, and for diverse tropical forests. Although progress is being made for the tropics (Schöngart et al., 2017), a full linkage of drought tolerance traits to drought responses would be invaluable for forecasting how little-known species and whole forests will respond to future droughts (Christoffersen et al., 2016; Powell et al., 2017).

As climate change drives increasing drought in many of the world's forests (Trenberth et al., 2014; Intergovernmental Panel on Climate Change, 2015), the fate of forests and their climate feedbacks will be shaped by the biophysical and physiological drivers observed here. Our results show that taller, more exposed trees and species with less drought-tolerant leaf traits will be most affected in terms of growth during the drought year. Survival is linked to resistance and resilience [**CHECK REFS**] (DeSoto et al., 2020; Gessler et al., 2020), implying it may be influenced by the same factors. Indeed, while the influence of PLA_{dry} and π_{tlp} on drought survival remains to be tested, taller trees have lower survival (Bennett et al., 2015; Stovall et al., 2019). As climate change-driven droughts affect forests worldwide, there is likely to be a shift from mature forests with tall, buffering trees to forests with a shorter overall stature (McDowell et al., 2020). At this point, species whose drought tolerance relies in part on existence within a buffered microenvironment (e.g., *F. grandifolia*) could in turn become more susceptible. Here, the relative importance of tree height *per se* versus crown exposure becomes crucial, shaping whether the dominant trees of shorter canopies are significantly more drought tolerant because of their shorter stature, or whether high exposure makes them as vulnerable as the taller trees of the former canopy. Studies disentangling the influence of height and exposure on drought tolerance will be critical to answering this question. Ultimately, distributions of tree heights and drought tolerance traits across broad moisture gradients suggest that forests exposed to more drought will shift towards shorter stature and be dominated by species with more drought-tolerant traits (Liu et al., 2019; Bartlett et al., 2016a; Zhu et al., 2018). Our study helps to elucidate the mechanisms behind these patterns, opening the door for more accurate forecasting of forest responses to future drought.

Author Contribution

KAT, IM, and AJT designed the research. Tree-ring chronologies were developed by RH under guidance of AJT and NP. Trait data were collected by IM, JZ under guidance of NK and LS. Other plot data were collected by IM, AS, EGA, and NB under guidance of EGA and WM. Data analyses were performed by IM under guidance of KAT and VH. KAT and IM interpreted the results. IM and KAT wrote the first draft of manuscript, and all authors contributed to revisions.

Supplementary Information

NEED TO UPDATE !!** Table S1. Monthly Palmer Drought Severity Index (PDSI), and its rank among all years between 1950 and 2009 (driest=1), for focal droughts.

Table S2. Species-specific bark thickness regression equations.

Table S3. Species-specific height regression equations.

Table S4. Individual tests of species traits as drivers of drought resistance, where Rt is used as the response variable.

Table S5. Individual tests of species traits as drivers of drought resistance, where Rt_{ARIMA} is used as the response variable.

Table S6. Summary of top full models for each drought instance, where Rt is used as the response variable.

Table S7. Summary of top models for each drought instance, where Rt_{ARIMA} is used as the response variable.

Figure S1. Time series of Palmer Drought Severity Index (PDSI) for the 2.5 years prior to each focal drought

Figure S2. Map of ForestGEO plot showing topographic wetness index and location of cored trees

Figure S3. Distribution of reconstructed tree heights across drought years.

Figure S4. Distribution of independent variables by species.

Figure S5. Comparison of Rt and Rt_{ARIMA} results, with residuals, for each drought scenario

Figure S6. Visualization of best model, with data, for all droughts combined.

Appendix S1. Further Package Citations

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